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Anatomical and Nutritional Adaptations of the Speckled Mousebird (*Colius striatus*)

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Folivory is a rare phenomenon in birds that has evolved independently in several lineages. It has been reported in ratites (Withers 1983, Herd and Dawson 1984), anatids (Buchsbaum et al. 1986, Dawson et al. 1989), ptarmigan (Gasaway et al. 1975), the Kakapo (*Strigops habroptilus;* Oliver 1955, Powlesland et al. 1992), and some species of *Saltator* (Bosque et al. 1999). The Hoatzin (*Opisthocomus hoazin*) is unique among birds in being the only documented foregut fermenter and the only obligate avian folivore (Grajal et al. 1989). Although folivory is common in mammals (Chivers and Langer 1994), the evolution of folivory in birds is constrained by body mass and the high mass-specific energy requirements of endothermy and flight, despite the apparent unlimited supply of fresh foliage in nature. Klasing (1998) defines an avian folivore as one that concentrates on leaves; however, the categories from an obligate folivore to a facultative folivore are poorly defined.

Folivory is associated with reduced food quality (Chivers and Langer 1994). Digestion costs for fermenting folivores are high owing to gut specializations (i.e. a fermentation chamber) and associated bacterial microflora for the breakdown of cellulose and release of volatile fatty acids (VFA; VanSoest 1983). Energy from a folivorous diet is released slowly, requiring a behavioral and physiological lifestyle that minimizes energy expenditure. Because energy requirements per unit body mass increase with decreasing body mass, small folivores have proportionally higher metabolic requirements relative to their gut capacity than do large folivores (Demment and VanSoest 1985). Consequently, small avian folivores have greater problems of energy acquisition than their larger avian counterparts and thus are expected to be rare.

Mousebirds, order Coliiformes, comprise six species that are endemic to sub-Saharan Africa (Maclean 1993). Despite the paucity of species, mousebirds are remarkably successful and have radiated into many habitats in Africa, occurring from harsh desert to moist savanna. The folivorous habits of these birds were first observed in the Speckled Mousebird (*Colius striatus;* Rowan 1967), although peculiarities of their thermoregulatory ability were noticed prior to this (McAtee 1947). Body temperatures of mousebirds are correlated with ambient temperature fluctuations, which is a putative reason for their nocturnal huddling behavior (Rowan 1967). Average body mass of each species is about 50 g, making mousebirds among the smallest of folivorous birds. Consequently, we investigated their gastrointestinal tract and digestive physiology and suggest how adaptations in these traits permit the combination of small size and folivory in birds. To determine the extent of morphological and physiological adaptations, we made outgroup comparisons with the Purple-crested Turaco (*Tauraco porphyreolophus*), which is a large forest frugivore, and with the Hoatzin.

Methods.—We collected 13 Speckled Mousebirds from Creighton (30°02'S, 29°46'E) and Pietermaritzburg (29°36'S, 30°24'E), South Africa, in May 1994

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TABLE 1. Body and gut dimensions of *Colius striatus*, *C. colius*, *Urocolius indicus*, and *Tauraco porphyreolophus*. Values are $\bar{x} \pm$ SE, with n in parentheses.

Parameter	*Colius striatus*	*C. colius*	*Urocolius indicus*	*Tauraco porphyreolophus*
Body mass (g)	50.7 ± 2.27 (13)	38.8 ± 0.4 (15)	50 (1)	318.1 ± 41.49 (4)
Esophagus length (mm)	44.1 ± 1.30 (13)	44.6 ± 0.7 (27)	30 (1)	64.2 ± 3.59 (4)
Proventriculus length (mm)	21.3 ± 0.99 (12)	17.2 ± 0.7 (27)	26 (1)	26.2 ± 2.21 (4)
Ventriculus length (mm)	21.9 ± 0.86 (13)	12.2 ± 0.5 (27)	14 (1)	31.6 ± 2.60 (4)
Ventriculus breadth (mm)	15.7 ± 0.67 (12)	14.1 ± 0.5 (27)	19 (1)	20.8 ± 3.78 (4)
Small intestine-cloacal (mm)	225.8 ± 7.54 (11)	169.0 ± 4.7 (27)	260 (1)	401.0 ± 38.15 (4)
Total GIT length (mm)	312.4 ± 8.59 (11)	244.0 ± 4.7 (27)	330 (1)	522.9 ± 38.36 (4)
GIT : HB index[a]	46.86 (11)		54.39 (1)	66.59 (4)
GIT : mass index[b]	61.42 (11)		70.65 (1)	59.09 (4)

[a] Length of small intestine to cloaca / cube root of head-body length (mm).
[b] Length of small intestine to cloaca / cube root of body mass (g).

and dissected the fresh specimens. Body measurements and gastrointestinal tract (GIT) dimensions were made with vernier calipers and a steel ruler (±0.5 mm). Under a dissecting microscope, we determined the proportion of leaf material, fruit, and seed in the ventriculus of each specimen. Sections of the GIT of *C. striatus* were fixed in 5% buffered glutaraldehyde at 4°C as initial preparation for scanning electron microscopy. The remaining sections of the GIT were fixed in Bouin's solution from which histological sections were prepared; these were stained with eosin haematoxylin to show the histological arrangement of the gastric epithelia. Immediately after dissection, the gut contents in the ventriculi of eight *C. striatus* were identified to food category as noted above and then placed in clear screw-top vials, frozen, and analyzed for VFAs using gas chromatography by the Animal Nutrition and Animal Production Institute, Irene, South Africa. Gut contents of the remaining individuals were spread on a glass slide and viewed using a dissecting microscope and percentages of food categories present estimated.

We dissected one Red-faced Mousebird (*Urocolius indicus*) and four Purple-crested Turacos obtained from the Durban Natural Science Museum to obtain GIT dimensions. Furthermore, 27 White-backed Mousebirds (*Colius colius*) collected in Prieska (29°39'S, 22°46'E) and Prince Albert (33°14'S, 22°02'E) by A. McKechnie were dissected for GIT dimensions. Gross morphology of the GIT of all specimens was examined using a dissecting microscope.

Results.—The structure of the GIT of the Speckled Mousebird consisted of an esophagus leading into a well-developed proventriculus that was composed of a muscular wall with a gross smooth inner surface except for a gracile reticulate pattern; no crop was evident. The proventriculus led to the ventriculus, which was simple, unilobular and thin-walled. The inner wall of the ventriculus was a mat of adpressed papillae. The surface area of the ventriculus of the Speckled Mousebird is large because of extensive convolutions. It also has some areas (>50%) that were pigmented black. The ventriculus *in situ* was a prominent organ, lying to the lower left side of the abdomen with the anterior dorsal portion slightly behind the posterior end of a liver lobe and the posterior dorsal portion lying directly against the dorsal body wall. The body wall was nonmuscular here and the skin pigmented black, with feathers on the exterior surface. The GIT length:body length index of Speckled Mousebirds was lower than that of the Purple-crested Turaco, whereas the GIT length:body mass index was higher (Table 1).

Both the Speckled Mousebird and the Purple-crested Turaco showed a typical gastric plan with mucosa, submucosa, and muscularis. In the Speckled Mousebird, the musculature was less extensively developed and showed no elastic tissue compared with the Purple-crested Turaco. The main difference between the two species was the extensive surface area in the ventriculus of the Speckled Mousebird owing to the extensive convolutions, whereas few convolutions were present in the Purple-crested Turaco.

Scanning electron microscopy revealed the ventriculus to be covered by speciose microbial flora. The microbial flora included spherical and ovoid bacteria arranged in long chains or pairs (possibly *Planococcus* or *Rumenococcus*; Sneath et al. 1986) and others that were rod-shaped. Further research is required to isolate, culture, and classify the microorganisms in the foregut of mousebirds.

We recorded the presence and concentration of VFAs in the proventriculus and ventriculus contents of Speckled Mousebirds: i.e. acetic acid, propionic acid, iso-butyric acid, n-butyric acid, iso-valeric acid, and n-valeric acid (Table 2). Small peaks indicating other VFAs were also seen.

The gut contents of Speckled Mousebirds varied widely in the amount of leaf material present (0 to 100%). A high proportion of fruit was eaten when leaf intake was low. The mean proportions (n = 10) of dietary categories in the ventriculus were 43.2 ± SE of 10.5% leaves, 54.3 ± 10.4% fruit, and 2.5 ± 2.5% seeds. We observed Speckled Mousebirds feeding on

TABLE 2. Volatile fatty acid concentrations (mmol/g 10^4) in the ventriculus of eight specimens of *Colius striatus*.

Acetic acid	Propionic acid	Iso-butyric acid	n-Butyric acid	Iso-valeric acid	n-Valeric acid
9.50	156.96	—	36.90	—	—
180.90	49.81	10.61	81.44	—	—
115.46	23.29	67.27	45.71	18.70	—
—	17.78	27.35	27.35	—	26.20
7.62	21.32	6.69	30.94	—	—
—	8.40	8.18	52.30	—	—
—	4.46	9.10	44.30	—	—
—	4.42	7.07	52.13	—	—

the leaves of various introduced plant species, including cultivated vegetables. In addition, we saw Speckled Mousebirds feeding on the leaves of native plant species, including *Erythrina lysistemon*, although fruit was available.

Discussion.—Unlike the Hoatzin (Grajal et al. 1989), GIT gross morphology of the Speckled Mousebird comprised an esophagus leading into a well-developed proventriculus with no clearly developed crop. The much larger Hoatzin has a gut capacity equivalent to 9% of total adult body mass (680 g) with a large double-chambered crop and a multichambered lower esophagus (together constituting 77% of total gut capacity; Grajal 1995b) that allows for high intake of food.

All foliage-fermenting vertebrates rely to variable degrees on microbes such as bacteria and protozoans to produce nutrients from cellulose (VanSoest 1983). Many avian herbivores can switch between a "fiber-skimming" strategy and a higher-efficiency fermentation strategy (Klasing 1998). The Hoatzin has a diverse microbial flora, including anaerobic bacteria and ciliate protozoans that appear to play an important role in nutrition (Dominguez-Bello et al. 1993). The Hoatzin is the only known bird with a high degree of fermentation in the crop, producing high levels of VFAs (Grajal et al. 1989, Grajal 1995a). Although not an obligate folivore, the Speckled Mousebird also has VFAs in its foregut, which probably are produced by the variously shaped bacteria found there. Although levels of VFAs that we found in Speckled Mousebirds are similar to those in Hoatzins (Grajal et al. 1989), much of the variation in VFA levels between individuals probably results from differences in the amount of leaf material ingested. Further research is required to determine the actual fermentation substrate and passage rates.

Unlike the Hoatzin, whose diet is 80% leaves (Grajal et al. 1989), the proportion of leaves in the diet of the Speckled Mousebird varied. However, Speckled Mousebirds in the laboratory can maintain body mass when feeding only on leaves (C. Downs unpubl. data). Considering the seasonal phenology of fruiting and the irregularity of fruit shortages, mousebirds should feed extensively on leaves when other food sources are scarce. Frugivores with fixed home ranges respond to periods of low fruit availability by increasing the proportion of non-fruits and aseasonal fruit types in the diet (Leighton and Leighton 1983). A disadvantage of microbial fermentation is the increase in transit time of food in the gut (Chivers and Langer 1994). Mousebirds appear to have overcome this by switching diets if higher-quality food is available. Gastrointestinal tract data for Red-faced Mousebirds and White-backed Mousebirds have been included for comparison (Table 1) because these species also are reported to feed irregularly on leaves. Further research is needed to test for the presence of bacteria and VFAs in the GITs of these species.

Hoatzins are very inactive compared with other bird species (Grajal and Strahl 1991). All Mousebirds exhibit heterothermia (Bartholomew and Trost 1970, Prinzinger 1988), and clustering behavior is an effective energy saver (Prinzinger 1988, Brown and Foster 1992) at night. Clustering during the daytime may be a resting behavior for these leaf-eating birds (Yamagishi and Kabango 1986). These factors can balance the tradeoff between a diet of low nutritional value and the high energy demands of flight and endothermy (Morton 1978).

Why, then, have mousebirds not evolved a larger body size to overcome thermal constraints? A temporally dynamic fruit-eating habit (when food is available) may be a response and means of obtaining extra energy. Folivory allows mousebirds to use a low-quality but freely available diet but requires specializations of the GIT. Because energy from leaves is not readily available, this small-sized folivore reduces energy demands with an energy minimization/conservation strategy. Mousebirds have labile thermoregulation (Bartholomew and Trost 1970, Prinzinger 1988) and reduce energy costs of flight through gliding (pers. obs.). In addition, the abundance of food requires less flying time and fewer searches for meals. This increases the amount of time available for basking and socializing. Speckled Mousebirds perch vertically, projecting their legs to facilitate sun basking and exposing the belly (and the gut) to the sun (pers. obs.). Mousebirds occur in groups, huddling to conserve energy and to avoid

the risks of roosting alone. Other small-to-medium-sized birds are considered facultative folivores because they include leaves in the diet seasonally (Al-Dabbagh et al. 1987, pers. obs.). Mousebirds adjust to seasonal fluctuations in food abundance by having a broad dietary tolerance and a propensity for folivory.

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